Clonal Variation in the Parthenogenetic Snail *Campeloma decisa* (Viviparidae)

BY

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INTRODUCTION

Recent studies of clonal diversity in parthenogenetic animals, as revealed by electrophoretic analysis of allozymic variation, have contributed to an understanding of processes involved in the evolution of non-Mendelian genetic systems (review in Lokki, 1976; Parker & Selander, 1976; Parker *et al.*, 1977). We here report on clonal diversity and genic heterozygosity in several populations of the parthenogenetic aquatic snail *Campeloma decisa* (Say, 1822) in central New York.

MATERIALS AND METHODS

Samples of *Campeloma* were collected by hand or by baiting with meat (Allison, 1942) at 5 localities in New York: Song Lake, near Syracuse, Onondaga County; west side of Jamesville Reservoir at Craner Oil Depot, Jamesville, Onondaga County; north end of Honeoye Lake, Livingston County; Delaware River at Walton, Delaware County; and Dryden Lake, near spillway east of Dryden, Tompkins County. Individual snails were processed for electrophoresis according to the techniques of Selander & Hudson (1976). Allozymic variation at 13 enzyme systems encoded by 21 structural gene loci was assayed by horizontal starch-gel electrophoresis (techniques described by Selander *et al.*, 1971). The following enzyme loci were scored: 3 leucyl-alanine peptidases (*Pep–1, –2, –3*), 2 leucine aminopeptidases (*Lap–1, –2*), 2 esterases (*Est–1, –2*), 2 phosphoglucomutases (*Pgm–1, –2*), phosphoglucose isomerase (*Pgi*), mannose phosphate isomerase (*Mpi*), β-glucuronidase (*β-Glu*), 2 superoxide dismutases (*Sod –1, –2*), α-glycerophosphate dehydrogenase (*α-Gpd*), glucose-6-phosphate dehydrogenase (*G6pd*), 2 malate dehydrogenases (*Mdh–1, –2*), 2 isocitrate dehydrogenases (*Idh–1, –2*), and 6-phosphogluconate dehydrogenase (*6-Pgd*). Electromorphs (corresponding to allelic variants) at variable loci were numbered according to their relative mobility, the most common being designated *100* in all cases. Average individual heterozygosity (*H*) was determined by direct count of heterozgotes.

RESULTS AND DISCUSSION

Nine of the 21 loci assayed were polymorphic in the 5 samples of *Campeloma* examined (Table 1). Two clones

Table 1

Genetic diversity in clones of *Campeloma decisa*

Locus[1]	Genotype	
	Clone I[2]	Clone II[3]
Pep-2	100/100	100/95
Lap-1	100/100	100/90
Lap-2	null	100/100
Est-1	100/100	100/90
Pgm-1	110/100	100/100
Pgm-2	100/100	110/100
Sod-1	100/100	105/100
α-Gpd	100/100	100/90
Idh-1	100/90	110/100

[1]The following loci were monomorphic for the same allele in both clones: *Pep-1, Pep-3, Est-2, Pgi, Mpi, β-Glu, Sod-2, G6pd, Mdh-1, Mdh-2, Idh-2,* and *6-Pgd.*

[2]Clone I: Song Lake, N = 30 specimens; Walton, N = 11; Dryden Lake, N = 38.

[3]Clone II: Jamesville Reservoir, N = 30; Honeoye Lake, N = 1.

(designated I and II) can be distinguished, and these differ at each of the 9 variable loci. The nature of the difference is such that only at one locus (*Lap–2*) do the clones not share an allele. The clones are monomorphic and indistinguishable at the remaining 12 loci. Thus, the clones differ genotypically at 43% of the loci examined, but share alleles at 95% of the loci.

The clones differ in level of individual heterozygosity, with Clone I having 2 of 21 loci fixed in heterozygous condition ($H = 9.5\%$), and Clone II having 7 of 21 loci fixed as heterozygotes ($H = 33.3\%$). The occurrence of fixed heterozygosity in one or both clones at 9 loci strongly suggests that *Campeloma decisa* has an apomictic system of egg maturation in which recombination does not occur (Uzzell, 1970; Nur, 1971), since, in the absence of heterotic selection, recombination in parthenogenetic lineages should lead to homozygosity (Asher, 1970). Mattox's (1937) cytological work on the related parthenogenetic form *C. rufum* was interpreted by Suomalainen (1950) as evidence that oögenesis is apomictic.

Without knowledge of the nature and extent of genetic diversity in the bisexual populations of *Campeloma* from which the parthenogens were derived, we can only speculate on the mode of origin of the clones. Because heterozygosity (and clonal diversity) is expected to increase in apomictic parthenogenetic lineages as a consequence of the accumulation of mutations (White, 1973; Lokki, 1976), it might be suggested that Clone II is older than Clone I. However, an alternative hypothesis is that the clones are equivalent in age but were derived from sexual individuals (belonging to the same or different populations) differing markedly in heterozygosity. A third possibility, which we regard as the least likely, is that the clones diverged genetically following the origin of a single parthenogenetic lineage from an individual of an ancestral sexual population.

Parthenogenetic forms of *Campeloma* apparently are confined to northeastern and north-central North America, while sexual species occur south of a line from Kentucky to Illinois (Mattox, 1938; Pollister & Pollister, 1940; Hubricht, 1943; Van der Schalie, 1965; Anderson, 1966). This pattern of distribution suggests the possibility that the parthenogens evolved and colonized northern areas at the time of recession of the last Pleistocene glacier. A similar interpretation has been advanced by Suomalainen (1962) to account for patterns of distribution of parthenogenetic insects in Europe.

Our findings for *Campeloma* are consistent with the results of previous work demonstrating that parthenogenetic "species" generally are clonally diverse (Suomalainen & Saura, 1973; Lokki *et al.*, 1975; Parker & Selander, 1976; Parker *et al.*, 1977). Each of the 4 populations for which we have reasonably adequate samples apparently consists of individuals belonging to one clone. Because populations of *Campeloma* are widely spaced and isolated in central New York, migration probably is infrequent, and colonization normally may involve the transport of only one or a few individuals. Hence, the uniclonal composition of populations may merely reflect the founder effect. However, the possibility that interclonal competition is involved should also be considered. For a number of parthenogenetic "species" and strongly selfing species, studies already reported or currently in progress in our laboratory suggest that local areas are inhabited by a small number of clones or strains that are genetically very divergent and differ in habitat distribution. For example, populations of the self-fertilizing land snail *Rumina decollata* in southern France are composed of 2 strains differing at 50% of their loci and showing "preferences" for relatively xeric or humid microhabitats (Selander & Hudson, 1976). Clones of the parthenogentic aquatic snail *Potamopyrgus jenkinsi* (Warwick, 1952; Winterbourn, 1970) differ at about half their loci (Selander & Jones, in preparation). Similarly, many populations of the parthenogenetic earthworm *Octolasion tyrtaeum* in central New York consist of 2 clones differing at 40% of their loci (John Jaenike, in preparation). This pattern suggests that limiting similarity (MacArthur & Levins, 1967; May & MacArthur, 1972) is involved in determining the extent of interclonal and interstrain diversity in local populations of parthenogenetic and selfing organisms. Our findings for *Campeloma* are consistent with the genetic aspect of this hypothesis, but the number of populations sampled is too small to provide evidence regarding possible clonal differences in habitat utilization. The hypothesis that clones or selfing strains can coexist only if they are rather divergent in genetically-determined adaptive traits related to differential niche utilization (or if they are minimally distinct genetically and, hence, ecologically equivalent or nearly so) is, of course, simply an extension of current theories relating to interspecific competition and resource partitioning. It can be tested through intensive study of the genetic and ecological relationships of parthenogenetic organisms such as *Campeloma*.

SUMMARY

Populations of the parthenogenetic aquatic snail *Campeloma decisa* in central New York consist of one of two clones differing genotypically at 43% of their structural gene loci and sharing alleles at 95% of the loci. The occurrence of fixed heterozygosity at 9 loci in one or both clones suggests a non-recombinational system of egg ma-

turation. Individual heterozygosity was 9.5% in one clone and 33.3% in the other. It is suggested that both the founder effect and ecological limiting similarity potentially are important factors determining the clonal structure of parthenogenetic "species."

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